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Field Observations on the Feeding of the Nudibranch *Gymnodoris* spp. in Japan

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Abstract. Here, we report field observations of the diets of some *Gymnodoris* species (Nudibranchia: Opisthobranchia) inhabiting warm waters in the vicinity of Japan. Some *Gymnodoris* species appeared to feed exclusively on a single species: *G. ceylonica* fed on *Nakamigawaia* sp.; *G. okinawae* on *Elysia* sp.; *G. striata* on *Elysia ornata*; and an undescribed *Gymnodoris* sp. fed on *Glossodoris cincta*. In contrast, other *Gymnodoris* species fed on multiple species: *G. citrina* fed on *G. okinawae* and eggs of nudibranchs; *G. inornata* fed on *G. rubropapulosa* and *Dendrodoris fumata*; and *G. rubropapulosa* fed on *Chromodoris annae*, *C. strigata*, *Chromodoris* sp., *Hypselodoris festiva*, and *Mexichromis multituberculata*.

INTRODUCTION

Except for some species of Cephalaspidea, Sacoglossa, and Anaspidea, opisthobranch mollusks are carnivorous. Each carnivorous opisthobranch feeds on particular prey items, e.g., sponges, hydroids, bryozoans, or ascidians. Some carnivorous opisthobranchs prey on other opisthobranchs and their eggs (see Behrens, 2005). These opisthobranch-feeding opisthobranchs include *Chelidonura* (Gosliner et al., 1996), *Navanax* (Paine, 1963), *Philinopsis* (Rudman, 1972), *Pleurobranchaea* (Battle & Nybakken, 1998), *Gymnodoris* (Kay & Young, 1969), *Roboastra* (Farmer, 1978), *Melibe* (Kay, 1979), and *Godiva* (Gosliner, 1987b). *Gymnodoris* species usually feed on opisthobranchs and/or their eggs, except for *Gymnodoris nigricolor*, which apparently lives on some species of goby (Osumi & Yamasu, 1994), such as *Amblyeleotris japonica* (Williams & Williams, 1986), by grasping the fins using their buccal apparatus.

Few studies have reported on the diets of other *Gymnodoris* species, particularly in their natural habitats. To date, diets have been reported for nine *Gymnodoris* species (Table 1). Some *Gymnodoris* species appear to feed exclusively on a single species, whereas others feed on multiple species. However, there is considerable doubt whether animals in the laboratory show their natural food habits. Therefore, data on the feeding behavior of *Gymnodoris* species should be collected in their natural habitat. To this end, we examined diets of some *Gymnodoris* species inhabiting warm waters in the vicinity of Japan.

MATERIALS AND METHODS

From 2000 to 2006, *Gymnodoris* species feeding on prey in their natural habitats were directly observed by SCUBA diving at Hachijo-jima Island, Tokyo (33°6′ N, 139°46′ E), Ohomi-jima Island,Yamaguchi (34°25′

Table 1

Summary of the proceeding studies on the diets of *Gymnodoris* spp.

Predator	Prey	Condition	Reference
Gymnodoris alba (Bergh, 1877)	*Aeolidiella* sp.	undescribed	Kay & Young, 1969; Kay, 1979
	Favorinus sp.	undescribed	Kay & Young, 1969; Kay, 1979
	Sakuraeolis modesta	laboratory	Hughes, 1983
	Flabellina alisonae	laboratory	Hughes, 1983
	Phyllodesmium sp.	laboratory	Hughes, 1983
Gymnodoris aurita (Gould, 1852)	*Marionia* sp.	field	Behrens, 2005
Gymnodoris bicolor (Alder & Hancock, 1866) (<*G. citrina*?)[1]	members of *Gymnodoris*	undescribed	Young, 1969
	Gymnodoris okinawae	undescribed	Young, 1969; Kay & Young, 1969; Kay, 1979
	the egg masses of *Gymnodoris okinawae*	undescribed	Young, 1969
	Gymnodoris plebeia	undescribed	Young, 1969; Kay & Young, 1969; Kay, 1979
Gymnodoris ceylonica (Kelaart, 1858)	*Stylocheilus longicauda*	undescribed	Johnson & Boucher, 1983
Gymnodoris citrina (Bergh, 1875)	*Gymnodoris citrina*	laboratory	Young, 1969
	Gymnodoris citrina	field	Johnson & Boucher, 1983; Johnson, 1992
	Gymnodoris okinawae	field	Johnson, 1992
	Gymnodoris plebeia	field	Johnson, 1992
	several *Gymnodoris* species	field	Johnson & Boucher, 1983
	unknown *Gymnodoris* spp.	field	Johnson, 1992
	eggs of other *Gymnodoris* species	field	Johnson & Boucher, 1983; Johnson, 1992
	eggs of *Gymnodoris ceylonica*	field	Johnson, 1992
Gymnodoris inornata Bergh, 1880	*Chromodoris orientalis*	laboratory	Hughes, 1983
	Doriopsilla miniata	laboratory	Hughes, 1983
Gymnodoris okinawae Baba, 1936	various species of the genus *Elysia*	undescribed	Kay & Young, 1969
	members of Elysiidae	undescribed	Young, 1969
	cephalaspidean	undescribed	Johnson & Boucher, 1983
	did not eat *Elysia*	laboratory	Johnson & Boucher, 1983
Gymnodoris rubropapulosa (Bergh, 1905)	*Hypselodoris iacula*	field	Behrens, 2005
Gymnodoris striata (Eliot, 1908)	*Plakobranchus ocellatus*	field and laboratory	Johnson & Boucher, 1983

[1] *Gymnodoris bicolor* (Alder & Hancock, 1866) is regarded as the junior synonym of *G. citrina* (Bergh, 1875) by many authors (e.g., Risbec, 1953; MacNae, 1958; Baba, 1960), although Young (1969a) described their internal morphologies discriminate *G. bicolor*.

N, 131°13′ E), Nagashima Island, Kagoshima (32°13′ N, 130°11′ E), Kinko-wan Bay, Kagoshima (31°33′ N, 130°37′ E), Aka-jima Island, Okinawa (26°12′ N, 127°17′ E), Gahi-jima Island, Okinawa (26°13′ N, 127°17′ E), and Zamami-jima Island, Okinawa (26°13′ N, 127° 17′ E). Predators and prey were identified by their external morphology and were photographed *in situ*. Body lengths were measured *in situ* using a ruler or determined from the photographs. We observed the following species: *Gymnodoris ceylonica* (Kelaart, 1858), *G. citrina* (Bergh, 1875), *G. inornata* Bergh, 1880, *G. okinawae* Baba, 1936, *G. rubropapulosa* (Bergh, 1905), *G. striata* (Eliot, 1908; > *G. amakusana* [Baba, 1996]), and an undescribed *Gymnodoris* sp. This undescribed species is often found around the Okinawa Islands and is recognized by its Japanese common name "Shirobonbon-umiushi" (cf. Ono, 2004).

RESULTS AND DISCUSSION

All feeding observations for *Gymnodoris* spp. are summarized in Table 2. We observed sixteen individuals of seven species of *Gymnodoris*. All individuals swallowed the prey whole, even if the prey's body length was the same as that of the predator. In one case of *G. citrina* (No. 3) and in two cases of *G. amakusana* (No. 14 and No. 15), the predators were smaller in body length than their prey and bit off pieces from the prey.

Johnson & Boucher (1983) reported that *G. ceylonica* feeds on the sea hare *Stylocheilus longicauda*; however, we believe they misidentified *S. striatus* (Quoy & Gaimard, 1832) as *S. longicauda*. Because of their similarity in body color, *S. striatus* is often misidentified as *S. longicauda* (Rudman, 1999a), but habitat use

Table 2

Gymnodoris spp. and their preys: field observation.

Predator	No.	Body length	Prey (body length)	Water temperature	Site[1]	Depth[2]	Habitat	Date
Gymnodoris ceylonica (Kelaart, 1858)	01	20 mm	*Nakamigawaia* sp. (8 mm)	NR	Aka Is.	6 m	sand	Summer, 2002
Gymnodoris citrina (Bergh, 1875)	02	20 mm	*Gymnodoris okinawae* (10 mm)	19°C	Hachijo Is.	5 m	rock, oecasional coral	6, February, 2002
	03	10 mm	*Gymnodoris okinawae* (18 mm)	20°C	Hachijo Is.	5 m	roek	April, 2003
	04	12 mm	eggs of nudibranch	NR	Gahi Is.	4 m	dead coral	May, 2001
Gymnodoris inornata Bergh, 1880	05	50 mm	*Gymnodoris rubropapulosa* (50 mm)	NR	Kinkoh Bay	15 m	rock, occasional sand	Autumn, 2002
	06	50 mm	*Dendrodoris fumata* (40 mm)	16.8°C	Kinkoh Bay	11 m	mud	8, January, 2006
Gymnodoris okinawae Baba, 1936	07	18 mm	*Elysia* sp. (18 mm)	20°C	Hachijo Is.	5 m	roek	April, 2003
Gymnodoris rubropapulosa (Bergh, 1905)	08	30 mm	*Chromodoris annae* (25 mm)	25°C	Hachijo Is.	NR	rock	November, 2004
	09	50 mm	*Chromodoris strigata* (30 mm)	27°C	Hachijo Is.	10 m	rock	18, June, 2000
	10	30 mm	*Chromodoris* sp. (20 mm)	25°C	Hachijo Is.	NR	rock	November, 2004
	11	30 mm	*Chromodoris* sp. (15 mm)	21°C	Haehijo Is.	5 m	roek	30, May, 2006
	12	30 mm	*Hypselodoris festiva* (15 mm)	25°C	Haehijo Is.	NR	rock	November, 2004
	13	50 mm	*Mexichromis multituberculata* (20 mm)	24°C	Gahi Is.	20 m	dead coral	May, 2000
Gymnodoris amakusana[3] (Baba, 1996)	14	20 mm	*Elysia ornata* (50 mm)	15°C	Ohmi Is.	6 m	muddy sand	21, December, 2003
	15	10 mm	*Elysia ornata* (40 mm)	12.5°C	Nagashima Is.	10 m	muddy sand, occasional rock	7, January, 2001
Gymnodoris sp.	16	60 mm	*Glossodoris cincta* (unknown)	22°C	Zamami Is.	15 m	sand	May, 2001

[1] See "materials and method" for details.
[2] NR, No record.
[3] Rudman (1999e) referred *G. amakusana* as a junior synonym of *G. striata*.

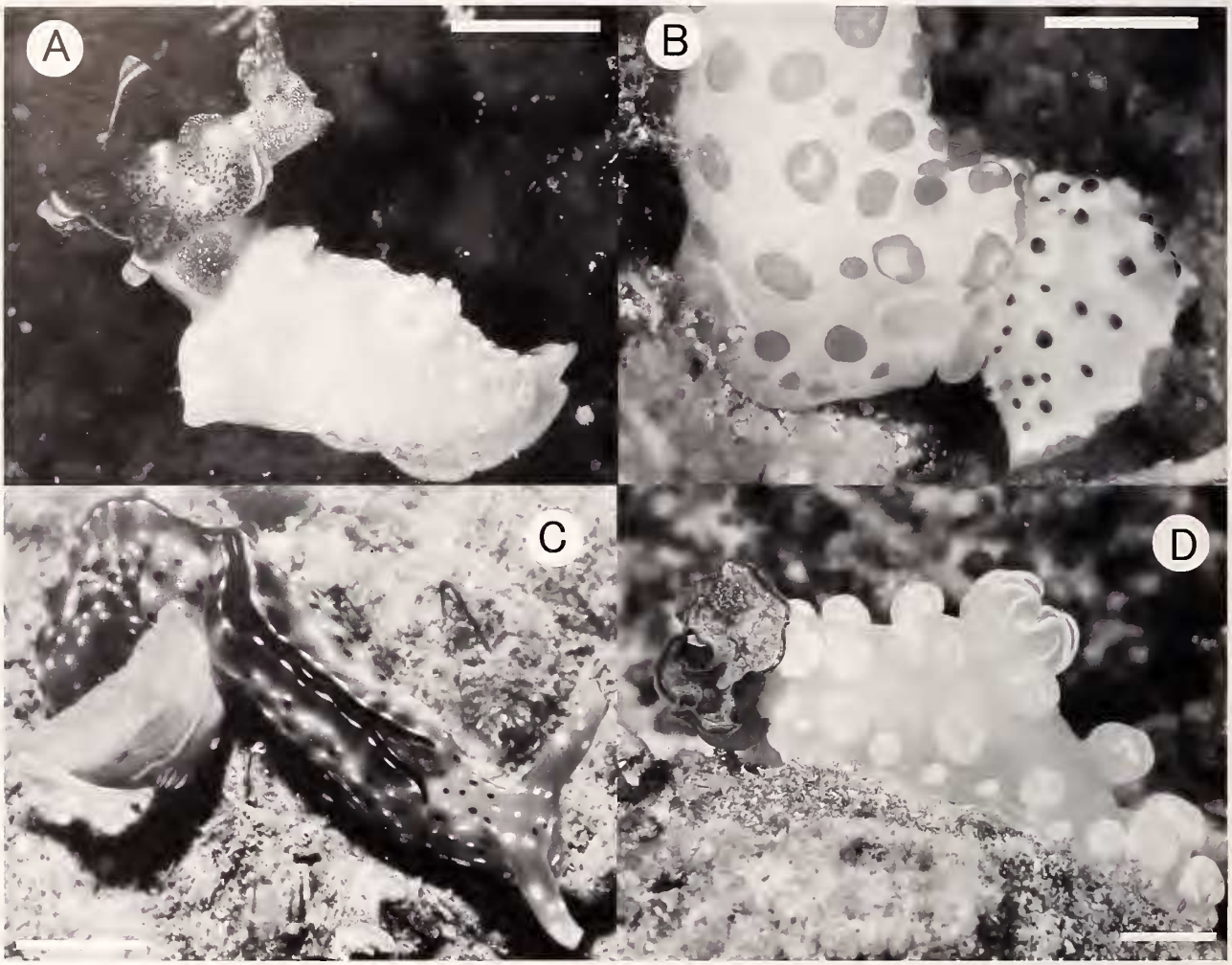

Figure 1. *Gymnodoris* species feeding on opisthobranchs in their natural habitats. (A) *G. okinawae* (right) feeding on a sacoglossan *Thuridilla* sp. (left). (B) *G. rubropapulosa* (left) feeding on *Mexichromis multituberculata* (right). (C) *G. anakusana* (left) feeding on *Elysia ornata* (right). (D) *Gymnodoris* sp. (right) feeding on *Glossodoris cincta* (left). Scale bars = 10 mm.

clearly differs between the species. *Stylocheilus longicauda* is usually found on drifting brown algae in the open ocean, where *G. ceylonica* never occurs (Rudman, 1999b), whereas *S. striatus* is benthic, and is often found with *G. ceylonica*. We observed that *G. ceylonica* feeds on *Nakamigawaia* sp. (Aglajidae, Cephalaspidea). This undescribed species is often found in Japan and is recognized by its Japanese common name "Kurobouzu" (cf. Ono, 1999). *Nakamigawaia* sp. is usually found on the sandy bottom. This observation indicates the possibility that *G. ceylonica* feeds not only on *S. striatus*, but also on other species in the same habitat.

Two individuals of *Gymnodoris citrina* fed on the congener *G. okinawae*, and one individual fed on the eggs of a nudibranch. *Gymnodoris citrina* was reported to feed on several *Gymnodoris* species, including *G. okinawae* and *G. plebeia*, in the field (Johnson & Boucher, 1983; Johnson, 1992), and on the eggs of congeners, such h as *G. ceylonica*, in the field and in aquaria (Young, 1967; Johnson & Boucher, 1983; Johnson, 1992). Moreover, *G. citrina* is cannibalistic. Young (1967) observed a 10-mm specimen consume a 6-mm specimen in an aquarium and reported that this occurrence was probably induced by unnaturally crowded conditions in the aquarium. However, Johnson (1992) observed this behavior in the field, in aquaria, and even in collecting jars, and concluded that cannibalism is normal behavior for *G. citrina*. Thus, it appears that *G. citrina* preys on several congeners and their eggs, as well as on conspecifics.

We observed that *Gymnodoris inornata* fed on *G. rubropapulosa* and *Dendrodoris fumata* in the field. In previous studies, *G. inornata* was reported to feed on

Chromodoris orientalis and *Dendrodoris miniata* (Hughes, 1983), but this was only observed in aquaria. Further field surveys are required to determine whether *G. inornata* feeds on these non-*Gymnodoris* species in nature.

In our field observations, *Gymnodoris okinawae* fed on *Thuridilla* sp. (Sacoglossa; Fig. 1A). This undescribed *Thuridilla* species is commonly found in southern parts of Japan, and is known by its Japanese common name "Fujiiro-midorigai" (cf. Ono, 2004). Kay & Young (1969) reported that *G. okinawae* fed on various species of *Elysia* (Sacoglossa). These observations suggest that *G. okinawae* preys on the sacoglossan family Elysiidae. In contrast, Johnson & Boucher (1983) reported that their specimens did not feed on several *Elysia* species in aquaria, but fed on small cephalaspideans in undescribed conditions. We do not know whether their specimens showed normal feeding behavior, because the habitat in which they were observed feeding, i.e., field or laboratory, was not described. Further field studies should be conducted to clarify whether *G. okinawae* feeds on cephalaspideans in nature.

We observed that *Gymnodoris rubropapulosa* fed on *Chromodoris strigata*, *Chromodoris* sp., *Hypselodoris festiva*, and *Mexichromis multituberculata* (Fig. 1B). Behrens (2005) reported that *G. rubropapulosa* fed on *H. iacula*. This species also fed on *Glossodoris rufomarginata*, *H. dollfusi*, *H. krakatoa*, and *M. marieri* (Behrens, personal communication). *Chromodoris* sp. is an undescribed species that is commonly found only in the vicinity of Hachijo-jima Island and the Bonin Islands, and is recognized by its Japanese common name "Kongasuri-umiushi" (cf. Nakano, 2004). These observations suggest that *G. rubropapulosa* feeds on various species of the family Chromodorididae. We observed that *G. amakusana* fed on *Elysia ornata* (Fig. 1C). In contrast, Rudman (1999c) referred to *G. amakusana* as a junior synonym of *G. striata*, which feeds on *Plakobranchus ocellatus* (Johnson & Boucher, 1983). If *G. striata* and *G. amakusana* are synonymous, they may show the same food habits. *Gymnodoris* sp. or Shirobonbon-umiushi differs from all other gymnodorids in shape and color (Rudman, 1999d). It has a white body with many large, puff-like pustules. We observed this species feeding on *Glossodoris cincta*. This is the first observation of its diet (Fig. 1D).

As described above, the diet of each *Gymnodoris* species encompasses a particular range of species. Some *Gymnodoris* species feed on various nudibranchs, whereas others have more selective diets. However, little is known about why and how *Gymnodoris* species identify and select their prey. For instance, Paine (1963) observed that the opisthobranch *Navanax inermis* locates its prey by contact (not distance) chemoreception via the mucus trail of the prey. It is unknown whether *Gymnodoris* species locate their prey using this same method. To gain a better understanding of the distinct food habits of these opisthobranch opisthobranch-feeders, we should determine how they detect and identify their prey, despite their low mobility.

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